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Integrating modelling of biodiversity composition and ecosystem function

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Abstract

There is increasing reliance on ecological models to improve our understanding of how ecological systems work, to project likely outcomes under alternative global change scenarios and to help develop robust management strategies. Two common types of spatiotemporally explicit ecological models are those focussed on biodiversity composition and those focussed on ecosystem function. These modelling disciplines are largely practiced separately, with separate literature, despite growing evidence that natural systems are shaped by the interaction of composition and function. Here we call for the development of new modelling approaches that integrate composition and function, accounting for the important interactions between these two dimensions, particularly under rapid global change. We examine existing modelling approaches that have begun to combine elements of composition and function, identifying their potential contribution to fully integrated modelling approaches. The development and application of integrated models of composition and function face a number of important challenges, including biological data limitations, system knowledge and computational constraints. We suggest a range of promising avenues that could help researchers overcome these challenges, including the use of virtual species, macroecological relationships and hybrid correlative-mechanistic modelling. Explicitly accounting for the interactions between composition and function within integrated modelling approaches has the potential to improve our understanding of ecological systems, provide more accurate predictions of their future states and transform their management.

Introduction

Modelling is becoming increasingly important in improving our understanding of ecological systems and our capacity to manage them sustainably into the future (Breckling et al. 2011). Ecological models can provide information on the present state of ecological systems, as well as knowledge of which factors are most important in influencing current patterns and recent trends (Wiegand et al. 2003). Ecological models can also be applied to project future ecological states under both acute and chronic perturbations, including habitat loss, anthropogenic harvesting and climate change (Evans 2012). Additionally, strategic application of ecological models provides the capacity to evaluate possible consequences of policy or management interventions and to identify those most likely to achieve goals for maintaining the diversity, structure and function of ecological systems into the future (CBD 2010).

Increasing recognition of the important role of ecological models has been accompanied by the development of a wide variety of modelling approaches (Breckling et al. 2011, Evans 2012). Our focus here is on models that make spatially and temporally explicit predictions across large regions (regional, continental, global) under alternative global change scenarios (e.g. Fig. 1), providing information relevant to the management of natural systems. While models operating at smaller spatial extents (site, landscape) are still valuable, here we focus on more general models that can be applied across the larger spatial extents at which spatiotemporal changes in biodiversity and ecosystem attributes under global change will play out, and the scales at which major policy, planning and management decision are often made. Each modelling technique within these bounds has unique objectives and methods, however, we suggest there are now two clearly discernible ecological modelling disciplines. The first focuses on modelling ‘biodiversity composition’ (Table 1), aiming to understand the identity and variety of

species over space and time (abundance, distribution, richness, turnover) (Noss 1990, Ferrier and Guisan 2006, Elith and Leathwick 2009). The second discipline focuses on modelling ‘ecosystem function’ (Table 1), where the interest is on the pools, fluxes, cycling and interactions of matter and energy in living systems (Evans et al. 2013). Obviously this dichotomy is not absolute, with some modelling approaches sharing attributes of both disciplines.

Spatiotemporally explicit modelling of biodiversity has focussed largely on understanding current patterns in diversity, identifying the main factors responsible for variation in diversity over space and time, and exploring how species persist, coexist and interact. The practical objectives of these modelling endeavours include identifying priority areas for conservation or management of species, and identifying species or areas most threatened by global change. A wide variety of techniques have been used to model biodiversity over space and time, including simple and complex models, based on either correlative (statistical) relationships or mechanistic processes. Examples include island biogeography theory (MacArthur and Wilson 1967), species distribution modelling (Elith and Leathwick 2009), metapopulation models (Anderson et al. 2009), models of community richness (Currie 2001) (Fig. 1a), community compositional turnover (Ferrier et al. 2007), community rank-abundance distributions (Dunstan and Foster 2011) and metacommunity models (Mokany et al. 2012).

In contrast, modelling of ecosystem function has focussed on understanding changes in the pools and fluxes of matter and energy through natural systems over space and time, including the role of different drivers, plus feedbacks between either the biotic and abiotic components, or between biophysical and anthropogenic components. The practical objectives of these models has typically been to inform sustainable

management of ecosystems in terms of the resources humans extract from them (e.g. fisheries, forestry, water), and the services they provide (e.g. climate buffering, pollination, soil stabilisation). Ecosystem function has typically been modelled using process-based approaches that consider dynamics of one or more trophic levels. Examples include terrestrial ecosystem models (Parton et al. 1987), dynamic global vegetation models (DGVMs: Sitch et al. 2003) (Fig. 1b), forest dynamics models (Botkin et al. 1972, Lischke et al. 2006), fire models (Liedloff and Cook 2007), ocean ecosystem models (Fulton et al. 2011) and global ecosystem models (Purves et al. 2013, Harfoot et al. 2014). While ecosystem models sometimes consider dynamics for one or more keystone species, or species of particular commercial interest, they do not deal individually (species by species) with the very large numbers of other species occurring within ecological communities (compositional diversity), or the role that diversity plays in mediating ecosystem function.

Here we chart a clear path for the development of new spatiotemporally explicit modelling approaches that integrate biodiversity composition and ecosystem function. While ecologists have long had a vision for such integrated models (Goudriaan et al. 1999), we are now in a unique position to overcome the lack of progress toward this goal. We identify a suite of potential benefits from new integrated modelling approaches, and review a variety of existing approaches that partially combine these two elements. Identifying the primary challenges in developing new integrated models then enables us to highlight a range of potential solutions and promising avenues for bringing together composition and function in spatiotemporally explicit models.

The need for integrated models of composition and function

The two modelling disciplines, focussing on biodiversity composition or ecosystem function, have essentially been viewing the same natural systems from different perspectives (Loreau 2010). In their mathematical representation of reality, each discipline is making alternative judgements regarding which components, processes and interactions are important and which can be simplified or ignored (Levins 2006). These alternative perspectives on real ecosystems may be sufficient in some situations, but are likely to be inadequate under the unprecedented, multi-dimensional global change most ecosystems now face, because altered composition and function are likely to interact, often in unexpected ways.

Observations, experiments and theory over the past two decades have demonstrated that compositional diversity can have a strong influence on ecosystem function ('Biodiversity Ecosystem Function' research: Schulze and Mooney 1993, Worm et al. 2006, Cardinale et al. 2012, Hooper et al. 2012). These effects are a consequence of a range of mechanisms, such as complementary resource use among species, or insurance effects over time (Naeem and Li 1997, Hooper 1998), with these processes becoming increasingly important as more ecosystem functions are considered over longer time periods (Isbell et al. 2011). Under rapid global change, simultaneous alterations to compositional diversity and environmental conditions could have important interactive consequences for ecosystem function (Cardinale et al. 2009, Wild et al. 2011).

Ecosystem processes can also strongly influence outcomes for biodiversity composition. A simple example is the capacity for disturbances such as fire, fishing, or logging, to cause major changes in the abundances or persistence of species and the diversity of communities, through direct impacts on populations and changes in the availability of resources (Shea et al. 2004, Frank et al. 2005). We also know that ecophysiological

processes often considered important for ecosystem function (growth, metabolism, predation, reproduction, mortality) can be crucial in influencing the occurrences and abundances of species (Kearney and Porter 2009). Indeed, most ecological processes will play some role in determining outcomes for both biodiversity composition and ecosystem function (Fig. 2).

Potential benefits of integrated models

We suggest that under the forces of rapid and intense global change, it becomes less certain how different ecological components and processes will interact, and which will be the most important in influencing outcomes. This provides a strong impetus to unite the two ecological modelling disciplines through novel integrated models. The development of new integrated modelling approaches could explicitly test the potential importance of interactions between elements of composition and function, as well as incorporate them into more realistic projections of future ecological states across large regions.

Projections from well-formulated integrated models may be more accurate and/or substantially different to those obtained from non-integrated models, which could alter our understanding of the threat posed by different global change drivers, and result in alternative management decisions being identified as most appropriate. By projecting outcomes for composition and function simultaneously, in a mutually consistent manner, integrated models would allow for more informed management decisions that could robustly consider co-benefits and trade-offs between composition and function, such as how to balance carbon sequestration, timber supply and biodiversity conservation through management of restoration or harvesting (Wintle et al. 2005, Miles and Kapos 2008). Integrated models of composition and function could also form

components within larger ‘Integrated Assessment Models’ (Harfoot et al. 2013), improving consideration of feedbacks between natural and socioeconomic systems. The strong emerging need for the development of integrated modelling approaches to better inform management is seen in the framework underlying the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) (Diaz et al. 2015) and its recognition of the importance of tools and methodologies for scenario analysis and modelling of biodiversity and ecosystem services (IPBES Deliverable 3c).

Potentially the strongest argument for the development of integrated models of composition and function is to improve our basic understanding of ecological systems and how they change over space and time. Models are powerful tools for combining our existing empirical knowledge with fundamental theory to extend our understanding of natural systems (Breckling et al. 2011). Integrated models could highlight priorities for the collection of new empirical data, identify gaps in our existing theories of how ecosystems work, and help develop new concepts for how biodiversity composition and ecosystem function interact.

Although we see a strong case for the development of integrated models, this does not mean existing approaches should be abandoned. There will be situations in which current independent modelling approaches will be sufficient, or even preferred. For example, to predict current patterns of biodiversity for a relatively intact region, existing correlative biodiversity modelling approaches may provide the simplest and most accurate predictions, given the relevant biogeographic processes are complex and have played out over deep ecological time. Similarly, projecting short-term changes in ecosystem function may be robustly achieved through an existing functional model, in situations where biodiversity effects might become more important over time (Isbell et

al. 2011). Where the benefits of an integrated modelling approach are unclear, the strategic development and application of such approaches could in itself provide a useful indication of when they are likely to be essential, desirable or unsuitable.

Existing modelling approaches incorporating both composition and function

We propose that the development of fully integrated models to project outcomes for large regions under alternative global change scenarios requires a new focus from ecological modellers, given there are no existing approaches that possess all the essential attributes of an integrated model (Table 2). However, we recognise there is a long history of ecological research relevant to integrating modelling of composition and function and there are a variety of existing modelling approaches that have in some way combined elements of composition and function. Here we do not attempt to comprehensively review this literature, but instead assess how existing approaches begin to bridge the gap between models of composition and function, help identify the major challenges to integration and highlight possible solutions.

Modellers starting from a biodiversity perspective have begun to add consideration of ecosystem function by incorporating projections of biodiversity composition with data on functional traits (D'Amen et al. 2015). For example, species distribution models have been combined with information on the functional attributes of each species to project climate change impacts on the functional diversity of plant and animal assemblages (Thuiller et al. 2006, Buisson et al. 2013). Similarly, correlative community-level models have combined compositional and functional trait information to project spatiotemporal change in community-level functional attributes (Dubuis et al. 2013, Mokany et al. 2015). The primary limitation of these approaches is their reliance on statistical relationships that do not account for the ecological processes important in

determining how both the composition and functional properties of communities interactively change over space and time.

Another approach has been to extend population models (e.g. Lotka-Volterra) to the metacommunity level, incorporating processes such as resource-use, competition, growth, productivity, mortality, dispersal, trophic interactions and evolution (Loreau et al. 2003, Tilman 2004, Loeuille and Loreau 2005, Gross and Cardinale 2007, Loreau 2010, Pillai et al. 2011). These theoretical models provide some of the best demonstrations of how composition and function may strongly interact, although their application to date has been limited to simulations within simple hypothetical systems (few species within few communities). Using these theoretical modelling approaches to make projections for real systems is strongly limited by the information required for each species and the large computational resources necessary to apply them over large highly diverse regions (Mokany and Ferrier 2011).

Partial integration of composition and function has also been achieved in a number of spatially-explicit ecosystem dynamics models. Typically, models of ecosystem dynamics apply functional groupings, with abundance or biomass considered within each group (e.g. DGVMs (Sitch et al. 2003), nutrient-phytoplankton-zooplankton models (Follows et al. 2007)). However, some ecosystem dynamics models consider each species separately, or combine fine and coarse functional categorisation (i.e. unique species plus functional groups). Examples of these approaches include forest gap models such as TreeMig (Lischke et al. 2006), marine ecosystem models such as Atlantis (Fulton et al. 2011) and more recent DGVM applications (Hickler et al. 2012). Such approaches can incorporate species-level compositional processes within models of ecosystem function, and hence provide information relevant to the conservation and

management of those species considered, as well as overall ecosystem function. This approach to integrating modelling of composition and function is restricted to considering a relatively small number of species rather than diversity more broadly, given the high diversity of most systems, shortfalls in our knowledge for most species, and current computational constraints (Boulangeat et al. 2012).

Key challenges in integrating modelling of composition and function

Limitations of biological data and knowledge

The amount of biological information currently available presents a significant challenge to the development and application of integrated models of biodiversity composition and ecosystem function. Only a fraction of the world's estimated 8.7 million species (Mora et al. 2011) are described, representing the first major data limitation, dubbed the 'Linnaean shortfall' (Brown and Lomolino 1998). For most of the species that are described, we have relatively sparse information on their distribution (the 'Wallacean shortfall': Lomolino 2004), their attributes and interactions with other species (the 'Hutchinsonian shortfall': Mokany and Ferrier 2011), or their phylogenetic relationships (the 'Darwinian shortfall': Diniz-Filho et al. 2013). Substantial information shortfalls also exist at the community level, in terms of spatial and temporal variation in the diversity, composition and structure of communities and food webs (Carpenter et al. 2006).

In developing and applying integrated models of composition and function, these biological data limitations constrain the possible ways in which models can be structured, parameterised, initialised and validated (Van Nes and Scheffer 2005). The number of parameters required for species or communities will need to be minimised for the sake of tractability, and potentially estimated using trait-based priors (Pollock et

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al. 2012) or existing macroecological theory (Brown et al. 2004). The role of biological data limitations can be reduced over time through continued empirical studies, technical advances in sampling methods (Horning et al. 2010, Shokralla et al. 2012) and making existing data more widely available (Evans et al. 2013). Recently established global experimental and observational research networks (Adler et al. 2011, Fraser et al. 2012, Duffy et al. 2015) are likely to have a particularly strong role to play in providing the datasets and knowledge required to develop, parameterise and validate integrated models. Despite these advances, for the foreseeable future, limitations in our knowledge will strongly shape the types of integrated models that can be developed and how the models can be tested or applied.

Balancing complexity and tractability

At large spatial scales, integrating biodiversity composition and ecosystem function within a single model would most likely require a more complex approach than most existing techniques that consider these aspects separately. Although this could be achieved by extending or coupling existing models (Fig. 3a), a potentially more robust approach involves developing customised models where the processes relevant to both composition and function are fully integrated (Fig. 3b). Such integration would likely result in more complex models, as gauged by the number of entities considered, interactions between entities, processes accounted for, the amount of mathematical formulae or computer code required to describe the model, and the time required to calibrate and validate the outcomes (Zellmer et al. 2006, Evans et al. 2013, Evans et al. 2013)

Historically, ‘simple’ ecological models were seen as preferable, being easier to formulate, parameterise, initialise, explore, understand, revise and replace (Peck 2004,

Van Nes and Scheffer 2005, Aumann 2007). However, there has been increasing advocacy for more realistic and complex ecological models (Grimm et al. 2005, Evans et al. 2013), given they may better capture the inherent complexity of ecosystems, their response to stochastic events, processes at multiple scales, local perturbations, historical forces and hence better inform robust management decisions (Fulton et al. 2003, Peck 2008). Integrated models will need to effectively balance these arguments in favour of complexity with the costs of model construction, the ease of parameterisation and analysis, the required accuracy of projections, the urgency for projections to be available and the potential costs of making the wrong management decision based on the model projections (Grantham et al. 2009, Runge et al. 2011).

The potential complexity of an integrated model can be managed in a number of ways, beginning with careful consideration of which processes to include and which biological levels to consider (Fulton 2010). For example, a major challenge for integrated models will be in accounting for the variety of interspecific interactions (e.g. trophic, competitive, facilitative) that we know are important in influencing both composition and function. Whilst in reality these interactions are between pairs of species, directly modelling every pairwise interaction would lead to a highly complex model, requiring many parameters, with associated uncertainty propagating through to the model predictions. More tractable approaches to accounting for interspecific interactions could involve generalisations based on functional traits or phylogeny (Kissling and Schleuning 2015).

Computational limitations

The development and application of integrated models for diverse and complex ecosystems is also constrained by currently available computational resources and the

skills of ecologists to harness them efficiently. Even if we possessed the biological knowledge to apply an existing ecosystem dynamics model with large numbers of distinct species, running such a model at sufficient spatiotemporal extent and resolution would be computationally prohibitive. This is due to current limits on how much data can be readily stored and accessed and the speed at which functions within a model can be processed (Cockshott et al. 2012), which is particularly important given that hundreds or thousands of simulations may be required to capture the ensemble of potential outcomes for a given global change or management scenario.

One common solution to existing computational constraints is the application of parallel processing, enabling models to run faster by harnessing multiple processors on either PCs or supercomputers. Unfortunately, the potential for parallel processing to speed-up an integrated model of composition and function will always be restricted by those model components that require serial implementation (Amdahl 1967), including interactive processes, such as herbivory, predation, dispersal, or learned/adaptive behaviour (Purves et al. 2013, Harfoot et al. 2014). Efficiencies could be gained through strategic shifts in the representation of biota within integrated models, aggregating to the functional group level for some processes (e.g. metabolism) and distilling to the species level for other processes (e.g. mortality, reproduction). The application of integrated models will be further enabled by avoiding model elements that will have high computation and memory requirements, through strategic use of efficient summaries, approximations (Evans et al. 2013), or coding techniques (Van Nes and Scheffer 2005).

Finally, the spatial and temporal resolution and extent for which an integrated model is to be applied will have a substantial impact on computational feasibility. Biodiversity

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composition is typically modelled on a finer spatial resolution than ecosystem function, given that individual species may respond to microclimates and persist within small areas (Potter et al. 2013). In contrast, models of ecosystem function tend to be implemented at a finer temporal resolution (hours, days, months) than those of biodiversity composition (years, decades, centuries), because of rapidly changing processes such as primary production or predation (Sitch et al. 2003, Fulton et al. 2011). An important challenge for integrated models will be devising approaches that marry the different spatial and temporal scales at which these two features are currently examined, allowing flexibility and the capacity to slide between scales in computationally efficient ways.

Promising avenues for developing new integrated models

Virtual species

We suggest that overcoming the substantial challenges in developing and applying integrated models of composition and function will require the development of novel approaches, or adapting and combining existing approaches in innovative ways. To overcome the shortfalls in our knowledge of biodiversity, the application of ‘virtual’ or ‘simulated’ species (Table 1) is likely to be extremely useful and often essential. There is a long history in ecology of applying models with virtual species, rather than real species with known attributes and distributions (Zurell et al. 2010), including testing or applying theoretical models (Hubbell 2001, Cabral and Kreft 2012), understanding biogeographic patterns (Rangel et al. 2007, VanDerWal et al. 2008), and assessing the adequacy or bias in different empirical sampling methods (Zurell et al. 2010). Virtual species have also been applied to predict biodiversity composition for large numbers of species (Mokany et al. 2011), and in implementing models of ecosystem function (Kleidon et al. 2009, Maury and Poggiale 2013).

In integrated models of composition and function, virtual species can be used within highly diverse and poorly studied taxonomic or functional groups. These virtual species can be allocated attributes, abundances and spatial distributions based on known statistical distributions and macroecological patterns (Jenkins et al. 2007, Smith et al. 2008) or relationships hypothesised from ecological theory (Brown et al. 2004). Where appropriate, virtual species could be combined with real species whose attributes and distributions are well known. This would include the larger, more abundant species in a group, which often have the greatest influence on the composition of communities and the functioning of ecosystems (Gaston 2010). The application of virtual species within integrated models of composition and function would require careful testing regarding the sensitivity of model outputs and processes to the estimated attributes.

Macroecological relationships

Harnessing existing knowledge regarding the macroecological relationships among species attributes is also likely to be useful in overcoming knowledge shortfalls and efficiently considering important ecological processes. A compelling example are the consistent relationships between the body size of species and a variety of attributes, including their abundance (White et al. 2007), range size (Gaston and Blackburn 1996), dispersal capacity (Thomson et al. 2011), metabolic rate (Brown et al. 2004), resource use (Brose et al. 2006), trophic interactions (Schramski et al. 2015), longevity (Hendriks 2007), and fecundity (Hendriks and Mulder 2008). These macroecological relationships could be used to estimate attributes for poorly studied or virtual species, and form a simple basis for modelled processes (Harfoot et al. 2014).

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Although macroecological relationships may have strong potential in filling knowledge gaps, care is required in applying them within integrated models of composition and function. While correlations between key attributes of species can be strong on a logarithmic scale, there is often several orders of magnitude variation around such macroecological relationships (Gaston and Blackburn 1999). The deviation of species from fundamental macroecological relationships, plus changes in the nature of macroecological relationships themselves (Supp et al. 2012), may have important implications for spatiotemporal patterns in the diversity and functioning of ecosystems.

Combining correlative and mechanistic elements

Along with statistical macroecological relationships, it may be necessary to combine other correlative model components with more mechanistic elements to implement integrated models of composition and function. Correlative model components are likely to be particularly useful for incorporating current patterns in the distribution of species and the composition of communities (Gaston 2000). Mechanistic modelling is more powerful in projecting changes in biodiversity composition and ecosystem function over time, under changing environmental conditions (Mokany and Ferrier 2011, Purves et al. 2013). Combining correlative and process-based model elements in ‘hybrid’ or ‘semi-mechanistic’ models is becoming increasingly common in projecting change in the distribution of species (Keith et al. 2008), the composition of communities (Mokany et al. 2012) and the functioning of ecosystems (Peng et al. 2002).

These recent approaches have demonstrated the utility of combining models of pattern and process, which is likely to help overcome knowledge shortfalls in integrated models, enabling their application over large regions, containing diverse and poorly-studied areas, taxa, or functional properties. Further development and application of

statistical mechanics approaches also offers much promise in combining correlative and mechanistic elements (Harte et al. 2008). Of particular value for integrated models could be extending hybrid approaches linking biodiversity composition with environmental drivers through functional attributes (Shipley et al. 2006, Laughlin et al. 2012).

Transforming knowledge and management through integrated modelling

One of the most compelling reasons for developing integrated models of biodiversity composition and ecosystem function is their potential to transform our knowledge of ecological systems and the way in which we manage them. Simply undertaking the process of developing and testing integrated models is likely to highlight gaps in existing concepts of how ecosystems work and consequently lead to new hypotheses and theories. While it is difficult to foresee the nature of these theoretical advances, one example where new theory may be required is in generalising the trade-offs in the many functional attributes and associated life history traits of species, which are likely to be important in influencing the coexistence of species as well as overall ecosystem function (Agrawal et al. 2010).

Applying integrated models of composition and function to large and diverse regions would also provide unique opportunities to further test, explore and develop the theory linking composition and function, which have emerged primarily out of local-scale empirical experiments (Cardinale et al. 2012, Hooper et al. 2012). Incorporating spatiotemporal processes in a dynamic integrated model would enable the extension and development of theory on the interaction between composition and function at metacommunity and metaecosystem scales. This would further advance the valuable contributions made by theoretical metacommunity models (Loreau et al. 2003, Pillai et

al. 2011) and provide information on the relative contribution of local and regional processes through which composition and function may interact (Mokany et al. 2013).

Integrated models of composition and function also have the capacity to transform management of ecological systems. Rather than simply relying on ‘trial and error’ to develop robust and adaptable policy and management (Schindler and Hilborn 2015), models can help identify the range of likely outcomes from alternative management action, incorporating uncertainty from wide variety of sources. Models are already widely used to inform the management of biodiversity and ecosystem function, including establishing new protected areas, setting fisheries quotas, managing threatened species and forestry operations (Wintle et al. 2005, Arkema et al. 2006, Fontes et al. 2010, Guisan et al. 2013). In situations where composition and function interact strongly to influence outcomes, models that do not account for this interaction would be less reliable, potentially suggesting management actions that could result in unintended consequences. Such situations may include managing alien invasive or range extending species, regulating fishing activities and developing strategies for controlling fire recurrence through prescribed burning. In these circumstances, the processes and management actions involved directly impact on both biodiversity composition and ecosystem function. Incorporating these feedbacks through integrated modelling could lead to more reliable projections of possible outcomes and transform the management of ecological systems by suggesting dramatically different management actions which meet objectives for both composition and function.

Conclusion

As the world changes rapidly, there is a growing need to improve our understanding of likely outcomes for ecological systems distributed over large regions and formulate

robust management approaches that best achieve our objectives for conserving biodiversity and maintaining healthy functioning ecosystems. There are clear and strong interactions between biodiversity composition and ecosystem function that need to be accounted for in the development of new integrated models. While integrating these two modelling disciplines faces substantial challenges, we see a variety of fruitful and innovative avenues for overcoming them. Developing, testing and applying integrated models of biodiversity composition and ecosystem function could improve our basic understanding of ecological systems, generate more reliable projections of likely outcomes across large areas under alternative future scenarios and transform our capacity to develop robust strategies for managing ecological systems. Achieving this vision is closer than ever, but it is a substantial scientific endeavour, requiring supportive research funding and collaborative commitment from diverse disciplines.

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Table Legends

Table 1. Definition of terms.

Term	Definition
Biodiversity composition	The identity and variety of species over space and time (abundance, distribution, richness, turnover) (Noss 1990).
Ecosystem function	Pools, fluxes, cycling and interactions of matter and energy in ecological systems (Evans et al. 2013).
Integrated model of composition and function	A model that simulates and projects simultaneous changes in biodiversity composition and ecosystem function over space and time for large regions, incorporating interactions between composition and function.
Virtual species	Application of ‘simulated’, ‘hypothetical’ or ‘artificial’ species that are generated for the purposes of a model, rather than being real named species with known attributes (Zurell et al. 2010).

Table 2. Proposed essential and desirable attributes of an integrated model of biodiversity composition and ecosystem function, and the degree to which a number of existing modelling approaches possess these attributes.

Proposed attribute of an integrated model	Examples of existing models					
	<u>ecosystem function</u>				<u>composition</u>	
	LPJ-GUESS	TreeMig	Atlantis	Madingley	M-SET	SESAM
<u>Essential</u>						
Spatially explicit	✓	✓	✓	✓	✓	✓
Temporally explicit (i.e. dynamic)	✓	✓	✓	✓	✓	✗
Fine spatial resolution (e.g. $\leq 1 \text{ km}^2$)	✗	✓	✗	✗	✓	✓
Fine temporal resolution (e.g. ≤ 1 month)	✓	✓	✓	✓	~	✗
Applicable across large extents (regional, continental, global)	✓	✓	✓	✓	✓	✓
Informed by current patterns in diversity	✗	~	~	✗	✓	✓
Informed by current patterns in structure / function	~	~	✓	~	✗	~
Considers important processes at the species level (e.g. physiological tolerances, local colonisation/extinction, dispersal)	~	✓	✓	✗	✓	~
Considers important ecosystem processes (e.g. photosynthesis, predation/herbivory, growth, disturbance)	✓	✓	✓	✓	✗	~
Considers all the diversity (species) within multiple taxonomic groups	✗	✗	~	✗	✓	~
Considers continuous variation in attributes between species	✗	✓	✓	✗	✗	✓
<u>Desirable</u>						
Modest amount of information/parameters required	✓	✗	✗	✓	✓	✗
Can be applied to any region or system	✗	✗	✗	✓	✓	✓
Easy to apply (e.g. freely available, desktop application)	✗	~	~	✓	✗	✗
Can explicitly incorporate human management actions	~	✓	✓	~	✓	~
Transparent and well documented	requires comparative assessment					
Fast run time (even over large regions)						
Easy to interrogate outputs / projections						

~ potentially; LPJ-GUESS (Hickler et al. 2012); TreeMig (Lishke et al. 2006); Atlantis (Fulton et al. 2011); Madingley (Harfoot et al. 2014); M-SET (Mokany et al. 2012); SESAM (D'Amen et al. 2015)

Figure Legends

Figure 1. Examples of ecological models predicting climate change impacts on plant communities across the globe, in terms of: **(a)** change in biodiversity composition (regional capacity for species richness), and; **(b)** change in ecosystem function (vegetation carbon content). For (a), a correlative model of plant species richness was used to project change in capacity for species richness (ΔCSR) to 2100 under the A1FI emissions scenario averaged across four GCM's (reproduced and adapted from Sommer et al. 2010). For (b) The dynamic global vegetation model LPJ was used to project change in vegetation structure and functioning to 2100 under the A2 emissions scenario and HadCM3 GCM (reproduced and adapted from Lucht et al. 2006).

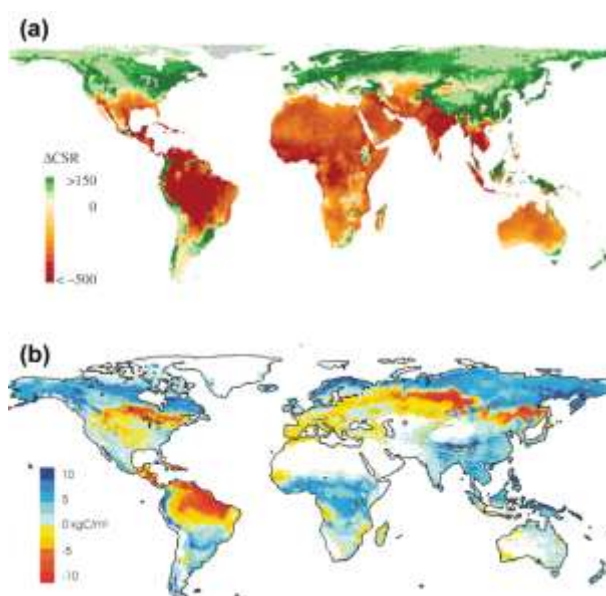


Figure 2. A range of important ecological processes and the degree to which they have been incorporated into existing models of either biodiversity composition or ecosystem function for real ecological systems (as indicated by their position and width). Single references are given as examples only, with none given where examples could not be found.

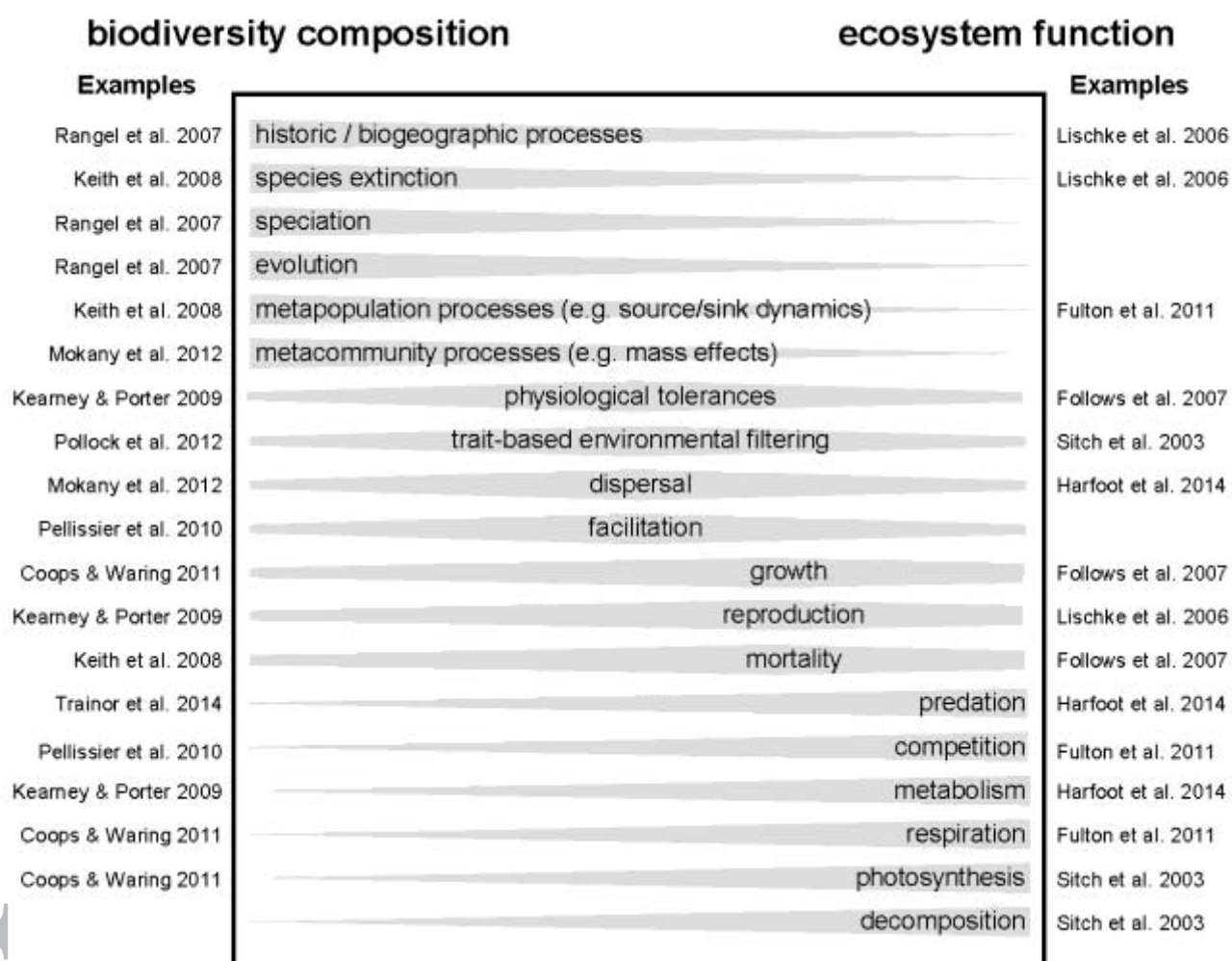


Figure 3. Alternative levels of combining consideration of biodiversity composition and ecosystem function within a spatiotemporal modelling approach: **(a)** existing separate models could be coupled, with predictions at key stages passing between otherwise separately operating models, or; **(b)** new models could be developed where processes and outcomes relevant to both composition and function are tightly integrated.

